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STAND DEVELOPMENT ON A 127-YR CHRONOSEQUENCE OF NATURALLY REGENERATING *SEQUOIA SEMPERVIRENS* (TAXODIACEAE) FORESTS

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Abstract

Understanding the natural patterns of regeneration following human disturbance is essential for effective restoration and management of second-growth forests. Despite their unique ecological character, little is known about these patterns in *Sequoia sempervirens* (D. Don) Endl. (Coast Redwood) forests. We examined the composition and structure of naturally regenerating stands with 360 randomly located sample plots across a chronosequence of five replicated age-classes (18 to 127 yr) and three old-growth reference sites. Results indicate a progression of stand characteristics towards old-growth conditions, with several measures reaching old-growth equivalence within the timeframe of the chronosequence. Stand density, canopy cover, and species richness reached old-growth equivalence within 41–80 yr; Shannon-diversity reached old-growth equivalence between 80–100 yr; and the density of redwood seedlings and shrub cover reached old-growth equivalence between 100–130 yr. Basal area, herb cover, and the relative dominance of *S. sempervirens* progressed toward, but did not reach, old-growth equivalence. Size-class analysis indicated an increase in the density of large diameter trees, with no change in the density of smaller size-classes after forty yr. Coast redwood associated understory species were favored on the older sites with the cover of *Calypso bulbosa* (L.) Oakes, *Trillium ovatum* Pursh, and *Viola sempervirens* Greene reaching old-growth equivalence, while *Iris douglasiana* Herb., *Tiarella trifoliate* L., and *Achlys triphylla* (Sm.) DC. did not. No non-native species were recorded in stands older than 60 yr. We conclude that coast redwood forests are resilient to human disturbance, though some old-growth characteristics may require more than a century to develop.

Key Words: Chronosequence, coast redwood, natural regeneration, second-growth, *Sequoia sempervirens*.

The coast redwood forest, dominated by *Sequoia sempervirens* (D. Don) Endl., is known for its high productivity, large carbon storage potential, and impressive stature (Preston 2007). Historically, *S. sempervirens* forests covered more than 8100 km^2 along the fog-shrouded coast from central California to southern Oregon. Due in large part to its value as a timber species, more than 95 percent of the original old-growth coast redwood forest has been converted into managed timber stands and other land uses (Noss 2000). With the majority of this forest type currently in second-growth, analysis of the natural patterns of stand development following timber-harvest is essential for effective management and restoration.

The dynamics of post-harvest development for *S. sempervirens* stands are unique among coniferous forests. *Sequoia sempervirens* possesses a natural resilience to disturbance due in part to its prolific vegetative sprouting ability (McBride 1977; Espinosa-Garcia and Langenheim 1991; Veirs 1996; Sawyer et al. 2000; Barbour et al. 2001). Though regeneration of *S. sempervirens* from seed can occasionally be abundant on mineral soils and fallen logs (Bingham and Sawyer 1988; Becking 1996; Porter 2002), the majority of recruitment results from vegetative sprouts, especially following timber harvest (Douhovnikoff et al. 2004; Lorimer et al. 2009). The vascular connection between vegetative sprouts and existing root structures results in competition between stems for apical dominance, rather than for individual tree survival (Kauppi et al. 1987; Burrows 1990; Sachs et al. 1993; Laureysens et al. 2003). Issues of overcrowding that slow the regeneration of other coniferous trees do not affect *S. sempervirens* in the same manner. Instead, redundant clonal stems senesce over time, thinning the stand naturally without the risk of stand-scale mortality (Floyd et al. 2009; Lutz and Halpern 2006; Sach et al. 1993). Survival of suppressed trees is also unusually high for *S. sempervirens* as epicormic sprouting increases stem production when understory trees are released (Finney 1993).

Old-growth *S. sempervirens* forests are relatively stable in terms of composition and structure (Busing and Fujimori 2002) and follow a 'gap phase' regenerative pattern where suppressed understory trees expand to fill canopy gaps created by individual, or small group, blowdowns (Sawyer et al. 2000). Natural stand-replacing disturbance events are extremely rare in *S. sempervirens* forests, even when compared to other coniferous forest types in the Pacific Northwest (Lorimer et al. 2009). As a result, the stand-scale removal of canopy through timber-harvest initiates regenerative patterns otherwise undocumented in this forest type.

Regeneration of *S. sempervirens* following timber harvest has been studied primarily in the context of post-harvest management practices such as planting, seeding, and thinning (Cole 1983; Oliver et al. 1994; Lindquist 2004a, b; Chittick and Keyes 2007; O'Hara et al. 2007). Very few studies have addressed the development of *S. sempervirens* stands in the absence of post-harvest management, and those that have been conducted focused on specific case studies or individual species rather than on forest regeneration as a whole (Boe 1965; Powers and Wiant 1970; Allen et al. 1996; Jules and Rathcke 1999).

Analysis of stand development of a long-lived species such as *S. sempervirens* (commonly exceeding 1500 yr in age) is best accomplished through the use of a chronosequence. This method has been routinely applied in other forest types (Crowell and Freedman 1994; Mund et al. 2002; Letcher and Chazdon 2009) as well as in *S. sempervirens* forests where they have been used to study specific impacts of logging (Loya and Jules 2007; Russell and Jones 2001; Russell 2009), but not over-all stand development. The objective of this study is to analyze natural regeneration of forest structure and composition in coast redwood forests, with the hypothesis that stand characteristics will tend toward old-growth conditions over time.

Methods

Study Sites

Data was collected in the central range of the coast redwood forest, as defined by Sawyer et al. (2000) (Fig. 1). Study sites were located primarily in the Big River watershed, consisting of more than 2968 hectares of previously harvested coast redwood forest in Mendocino Co., California (California Department of Parks and Recreation 2006). Much of the watershed was managed as industrial timberland prior to its purchase by the Mendocino Land Trust in 2002, and subsequent transfer to the California State Parks as the Big River Unit of Mendocino Headlands State Park. The Big River watershed was an ideal location for this study due to the presence of second-growth redwood stands ranging from 15 to 127 yr old that had received no post-harvest manipulation.

The vegetation of the area is characteristic of the central range of the coast redwood forest with *Sequoia sempervirens*, *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*, and *Abies grandis* (Douglas ex D. Don) Lindl. dominating the canopy, and *Lithocarpus densiflorus* (Hook. & Arn.) Rehder and *Tsuga heterophylla* (Raf.) Sarg. commonly occurring in the subcanopy. Understory shrub species include *Polystichum munitum* (Kaulf.) C. Presl, *Vaccinium ovatum* Pursh, and *Rhododendron macrophyllum* D. Don. Common herbaceous understory species include *Oxalis oregana* Nutt., *Trillium ovatum* Pursh, *Viola sempervirens* Greene, *Calypso bulbosa* (L.) Oakes, *Iris douglasiana* Herb., *Tiarella trifoliata* L., and *Achlys triphylla* (Sm.) DC. The soils of the area are derived from the Franciscan assemblage, consisting mainly of sandstone and marine sediments. Typically, winters are cool and wet with an annual precipitation of 2500 mm or more (Sawyer et al. 2000). Summers are mild with moisture from intermittent fog providing up to 30% of the water requirements of *S. sempervirens* each year (Burgess and Dawson 2004).

For inclusion in this study, each site was required to have been previously clear-cut, be large enough for adequate sampling without edge effects (Russell and Jones 2001), and have not received post-harvest management such as seeding, thinning, or planting. Using these criteria, three study sites were selected in each of the five post-harvest age-classes (0–20, 21–40, 41–60, 81–100, and 101–130 yr) as well as the three unharvested old-growth reference sites. The post-harvest age-class 61–80 yr was not sampled due to a lack of sites in that age range that met the criteria of this study. Sites were selected using detailed timber harvest and land management history maps on a GIS platform (Rutland 2002). Old-growth reference sites included Montgomery Woods State Natural Reserve (462 ha) located in the Big River watershed; Russell Unit (49 ha) of Mendocino Headlands State Park located in the Brewery Creek watershed adjacent to the Big River Unit; and Hendy Woods State Park (342 ha) located in the Navarro River watershed to the south of the Big River. These three sites were selected because they represent the only sizable remaining old-growth stands in Mendocino County.

Data Collection

Twenty, 0.031 ha (20 m diam.), circular sample plots were randomly selected within each of the 18 study sites, and located using a handheld GPS receiver. Each sample plot was placed a minimum of 20 m from adjacent plots, 10 m from special habitats such as riparian areas and rock outcroppings, and 200 m from adjacent age-class boundaries and main access roads. Plot size and sampling intensity were determined through a pilot study using the species-area curve method (Cain 1938) and are consistent with previous

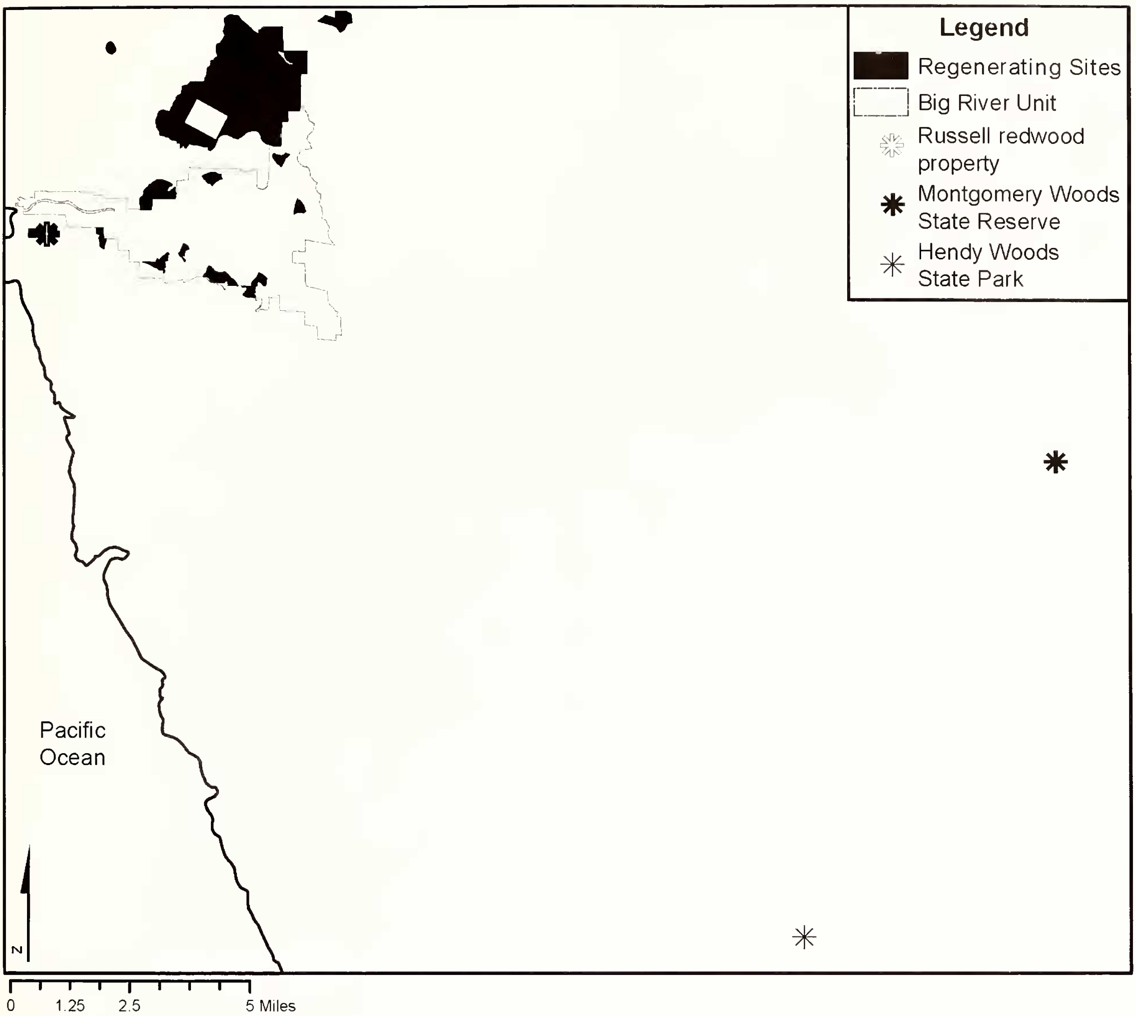

FIG. 1. Location of sampled regenerating stands and old-growth reference sites in Mendocino County, California.

research conducted in this forest type (Russell and Jones 2001; Loya and Jules 2007).

Data collected on each plot included: tree canopy cover (measured at plot center using a spherical crown densiometer with one reading taken in each of the four cardinal directions); the occurrence and abundance of each tree species; the diameter (measured at 1.4 m above ground level) of all individuals greater than one meter in height; and the occurrence and abundance of all tree seedlings. The percent cover for all understory species, including both herbs and shrubs, were determined using ocular estimates over the entire plot. In order to improve the accuracy of estimates plots were divided into eight sample wedges. Cover of each species was estimated in the field by two researches and averaged. Species were identified using the Jepson manual of higher plants of California (Hickman 1993).

Data Analysis

As a preparatory procedure prior to conducting ANOVA, we constructed a correlation matrix to examine possible relationships between stand characteristics and stand age. Significant correlations were found for several variables including tree density, seedling density, basal area and dominance of tree species, canopy cover, shrub cover, herbaceous cover, species richness, Shannon-diversity (Weaver and Shannon 1949), and the cover of individual understory species including non-natives. One-way ANOVA analysis was used to test for differences among the means for each variable between age-classes and old-growth reference sites in a manner consistent with analysis of chronosequence data in other forest types (Pare and Bergeron 1995; Claus and George 2005; Delzon and Loustau 2005). Data

TABLE 1. STAND CHARACTERISTICS OF SIX AGE-CLASSES IN A CHRONOSEQUENCE OF POST-HARVEST DEVELOPMENT IN THE CENTRAL RANGE OF THE *SEQUOIA SEMPERVIRENS* FOREST. Age-classes sharing the same lower-case letter in each series were not significantly different, based on single factor ANOVA analysis ($\alpha = 0.05$).

Age class	Tree density (trees/ha)	Combined seedling density (seedlings/ha)	Redwood seedling density (seedlings/ha)	Basal area (m^2/ha)	Richness (species/plot)	Shannon-diversity
0–20 yr	2048 a	890 a	184 a	14.8 a	21.9 a	2.0 a
21–40 yr	1889 a	1152 b	291 a	22.9 b	18.4 b	2.0 a
41–60 yr	940 b	1243 b	311 a	55.3 c	18.6 b	2.2 b
81–100 yr	1260 c	1189 b	338 a	96.9 d	17.9 b	1.9 c
101–130 yr	906 b	829 a	516 b	102.5 e	18.0 b	1.9 c
Old-growth	763 b	917 a,b	643 b	362.2 f	16.9 b	1.8 c

were tested for homogeneity using the Bartlett's Chi-Square statistic, and post-hoc analyses were conducted using the Bonferroni test for pair-wise differences between groups. Principle components analysis (PCA) was used to characterize general trends in species cover between age-classes. PCA data was transformed with individual variable ranking to eliminate null values. Data analyses were conducted using Aable 2 statistical software (Gigawiz Ltd. Co., Tusla).

RESULTS

Tree Density, Dominance, and Diameter Distribution

The density of trees (>1 m in height) declined with stand age (Table 1). The highest density was measured in the two youngest age-classes with significantly lower densities found in all other age-classes. Initial statistical equivalence with old-growth reference sites was reached in the third age-class suggesting the occurrence of a natural thinning event up until 40 yr. Somewhat higher densities on the two oldest age-classes, compared to the old-growth, suggest that stand thinning may continue at a reduced rate as the forest transitions toward old-growth conditions.

The combined density of tree seedlings exhibited little variation between age-classes. A somewhat higher number were found on sites ranging from 21–100 yr, however, all age-classes were statistically equivalent to old-growth. The density of *S. sempervirens* seedlings, however, exhibited a positive trend with stand age with the highest density found on the old-growth reference sites; statistical equivalence with old-growth was found for sites over 100 yr. No statistically significant relationship was found between stand age and the density of any other trees seedlings.

The average combined basal area per hectare increased with stand age exhibiting significantly higher values in each successive age-class (Table 1). Basal area did not reach statistical equivalence with old-growth stands within the timeframe of the chronosequence. Analysis of the relative dominance (specific basal area/total basal area) of the three most common tree species (*S. sempervirens*, *L. densiflorus*, and *P. menziesii*) indicated an increase in the relative dominance of *S. sempervirens* over time (Fig. 2), with *S. sempervirens* eclipsing all other species in the

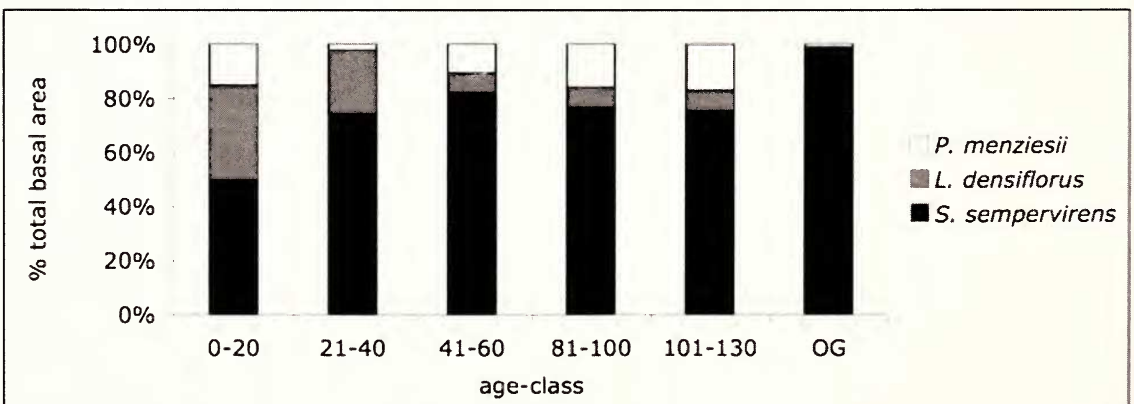

FIG. 2. Relative dominance (specific basal area/total basal area) of *Sequoia sempervirens*, *Lithocarpus densiflorus*, and *Pseudotsuga menziesii* across a 127-yr chronosequence of naturally regenerating *Sequoia sempervirens* stands.

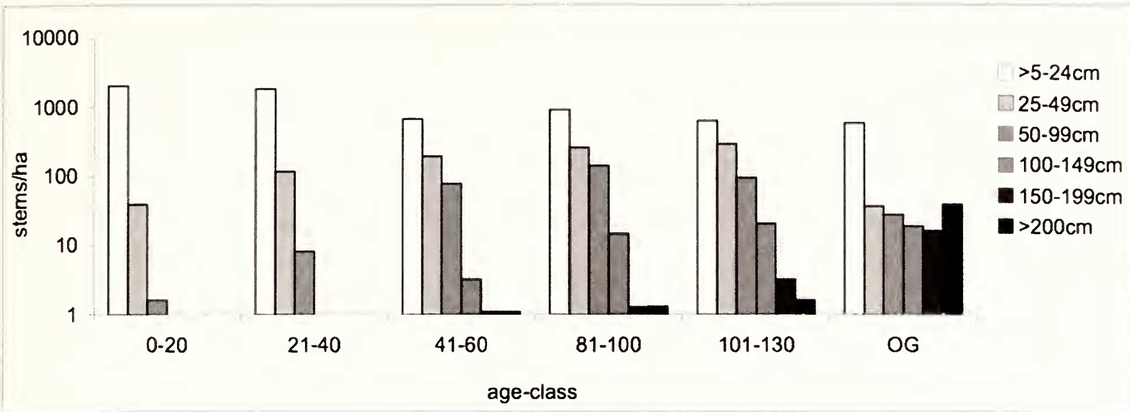

FIG. 3. Diameter distributions between six age-classes for all tree species combined on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest.

old-growth age class. The highest relative dominance for *L. densiflorus* was found in the two youngest age-classes, with significantly lower values found for all subsequent age-classes. The relative dominance of *P. menziesii* varied throughout the chronosequence with its highest values found in the 81–100 yr and 100–130 yr age-classes.

An analysis of diameter distributions, based on size classes defined by Guisti (2007), indicated an increase in the density of larger diameter trees over time (Fig. 3). The density of the smallest size-class of tree declined significantly in the early age classes, but showed no significant change after 40 yr. This result is consistent with a natural thinning event occurring early in the stand development process. Individual analysis of the diameter distributions of the three most common tree species (*S. sempervirens*, *L. densiflorus*, and *P. menziesii*) suggests a pulse of regeneration for each species early in the chronosequence (Fig. 4). It was also noted that *S. sempervirens* had the

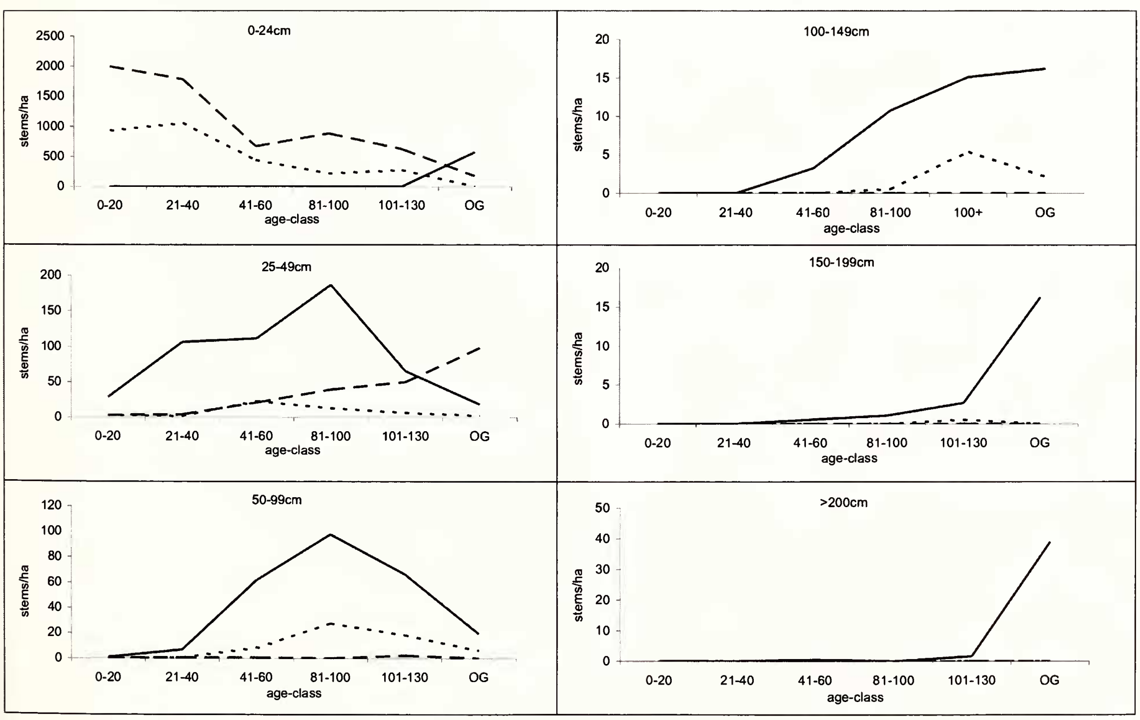

FIG. 4. Diameter distribution of three species on six age-classes combined on a post-harvest chronosequence in the central range of the coast redwood forest (solid line = *Sequoia sempervirens*; wide-dashed line = *Lithocarpus densiflorus*; narrow-dashed line = *Pseudotsuga menziesii*).

highest density of trees in all size-classes across the chronosequence with the exception of the smallest size-class (0–24 centimeter) where *L. densiflorus*, and *P. menziesii* dominated, and the 25–49 centimeter) size class where *P. menziesii* dominated in the old-growth.

Percent Cover of Canopy Layers

The percent cover of trees, shrubs, and herbs varied significantly between age-classes (Fig. 5). The lowest tree cover was recorded in the two youngest age-classes with cover statistically equivalent to old-growth found in stands older than 81 yr. Shrub cover was highest in the two youngest age-classes, significantly lower in the 41–60 yr age-class, and progressively higher thereafter, reaching statistical equivalence with old-growth in the two oldest age-classes. Herb cover was uniformly low, and statistically equivalent, in all second-growth sites compared to old-growth where it was more than three times greater.

Diversity and Species Distribution

One hundred twenty-seven plant species were recorded in the sample plots (Appendix 1). The highest species richness (species/plot) was found in the youngest age-class with lower, statistically equivalent, values in all other age-classes including old-growth (Table 1). The Shannon-diversity index (H′) also exhibited a generally negative trend reaching statistical equivalence with old-growth in stands 81 yr and older. An H′ peak was found for the 41–60 yr age class, possibly in response to the natural thinning event noted in the earlier age-classes.

Principal components analysis, using ranked percent cover of the 55 most common species, produced two axes that together explained 53.3% of the total variance with the first axis accounting for 35.9% and the second axis accounting for 17.4% (Fig. 6). The ordination illustrates grouping by age-class along the x-axis (PC 1) with positive eigenvalues associated with the oldest age-classes including *S. sempervirens* (0.33), *Trillium ovatum* (0.45), *Oxalis oregana* (0.36), *Viola sempervirens* (0.34), *Tiarella trifoliata* (0.32), and *Calypso bulbosa* (0.28); and negative eigenvalues associated with the younger age classes including *Lithocarpus densiflorus* (−0.31), *Lonicera hispidula* Douglas (−0.34), *Whipplea modesta* Torr. (−0.32), and *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (−0.27). The y-axis (PC_2) was positively associated with *Vaccinium ovatum* (0.41) and *Rhododendron macrophyllum* (0.30); and negatively correlated with *Sequoia sempervirens* (−0.31) and *Oxalis oregana* (−0.31).

Ten non-native plant species were recorded within the chronosequence (Table 2). The cover of each of these species declined with stand age to the extent that no non-native species were recorded in stands older than 60 yr. The absence of non-natives in the older age-classes suggests a lack of successful long-term establishment. However, the year of introduction, and historic distribution of each species, must also be considered as a possible explanation for their absence in older stands. While species such as *Sonchus asper* (L.) Hill and *Stellaria media* (L.) Vill. have been present in the region since the middle of the 1800's, *Cortaderia selloana* (Schult.) Asch. & Graebn. and *Leontodon leysseri* (Vill.) M-rat may not have been present until the middle of the 1900's.

Additional analysis of understory species cover indicated that several species commonly associated with coast redwood forests increased with years since harvest. The cover of *C. bulbosa*, *T. ovatum*, and *V. sempervirens* increased to levels statistically equivalent to the old-growth reference sites within the timeframe of the chronosequence (Fig. 7a). The cover of *Iris douglasiana*, *Tiarella trifoliata* L., and *Achlys triphylla* also exhibited positive trends with stand age, but were significantly lower on all age-classes compared to old-growth (Fig. 7b).

Discussion

In contrast to the "gap phase" succession process associated with old-growth coast redwood forests, the second-growth stands studied in our post-harvest chronosequence followed patterns similar to forest types that regularly experience stand scale disturbance. Results indicate a progression through the four phases of succession outlined by Oliver (1981), "stand re-initiation," "stem exclusion," "understory re-initiation," and "old-growth." Many stand characteristics including tree density, canopy cover, shrub-cover, species diversity, non-native species occurrence, and the cover of several redwood associated species reached old-growth equivalence. While total basal area, dominance of *S. sempervirens*, herb cover, and the cover of several other redwood associated species, all progressed toward, but did not reach, old-growth equivalence within the 127-yr timeframe of the chronosequence. In addition, the diameter distribution of trees within age-classes indicated a transition from stands characterized by a high density of small trees, to stands exhibiting a mixed size-class distribution. These results are consistent with the view that forests dominated by *S. sempervirens* have a high regenerative potential and are highly resilient following disturbance (Allen et al. 1996).

The assertion that natural processes of community development are sufficient management approaches for the regeneration of coast redwood

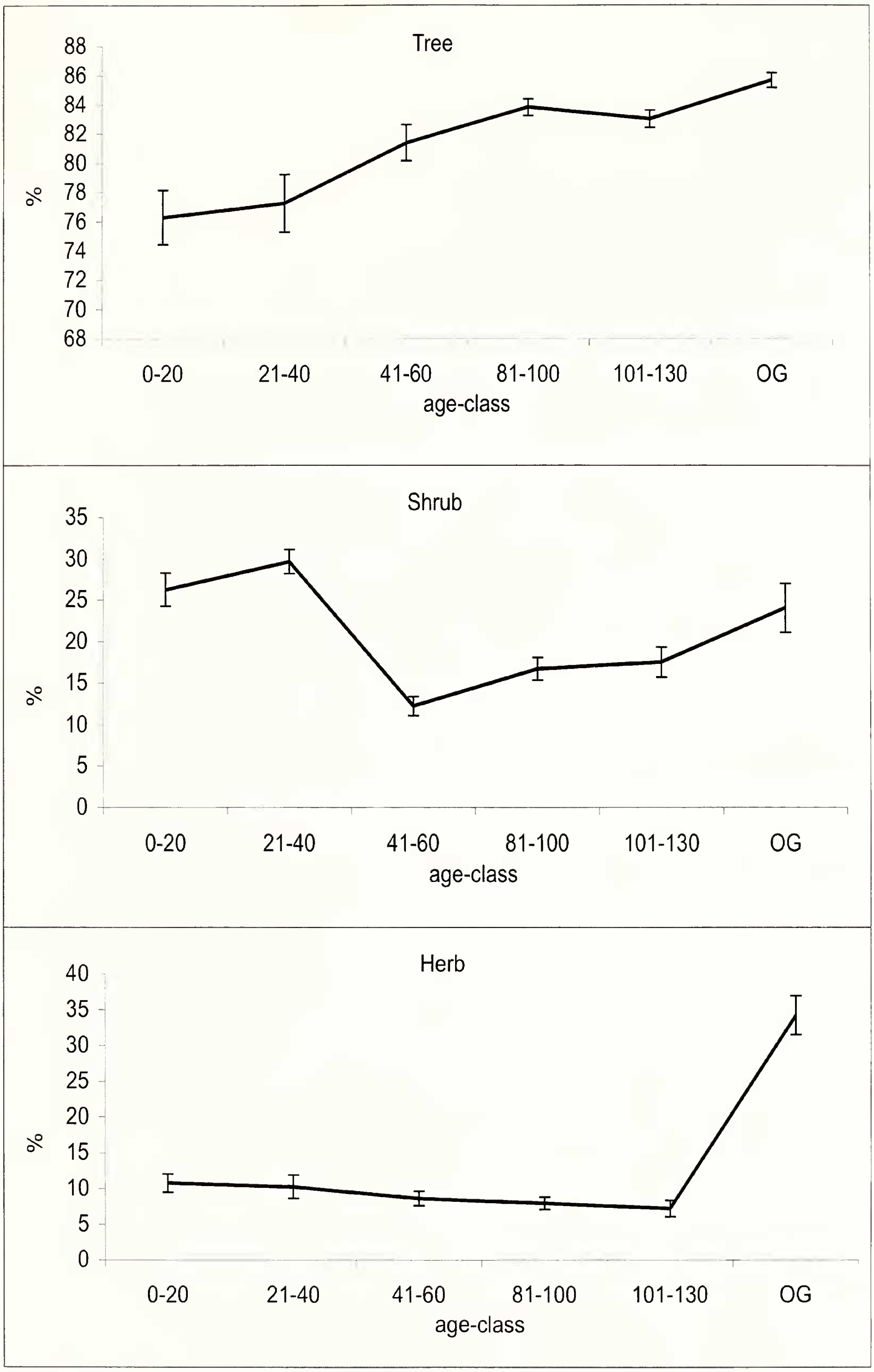

FIG. 5. Percent cover of trees, shrubs, and herbs on six age-classes on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest; error bars indicate standard error.

forests (Busing and Fujimori 2002, 2005) is also supported by this research to some degree. The proliferation of *Trillium ovatum*, a species that is severely impacted by timber harvesting (Kahmen and Jules 2005), as well as several other coast redwood associates within the timeframe of our chronsequence, is encouraging. However, not all coast redwood-associated species recovered com-

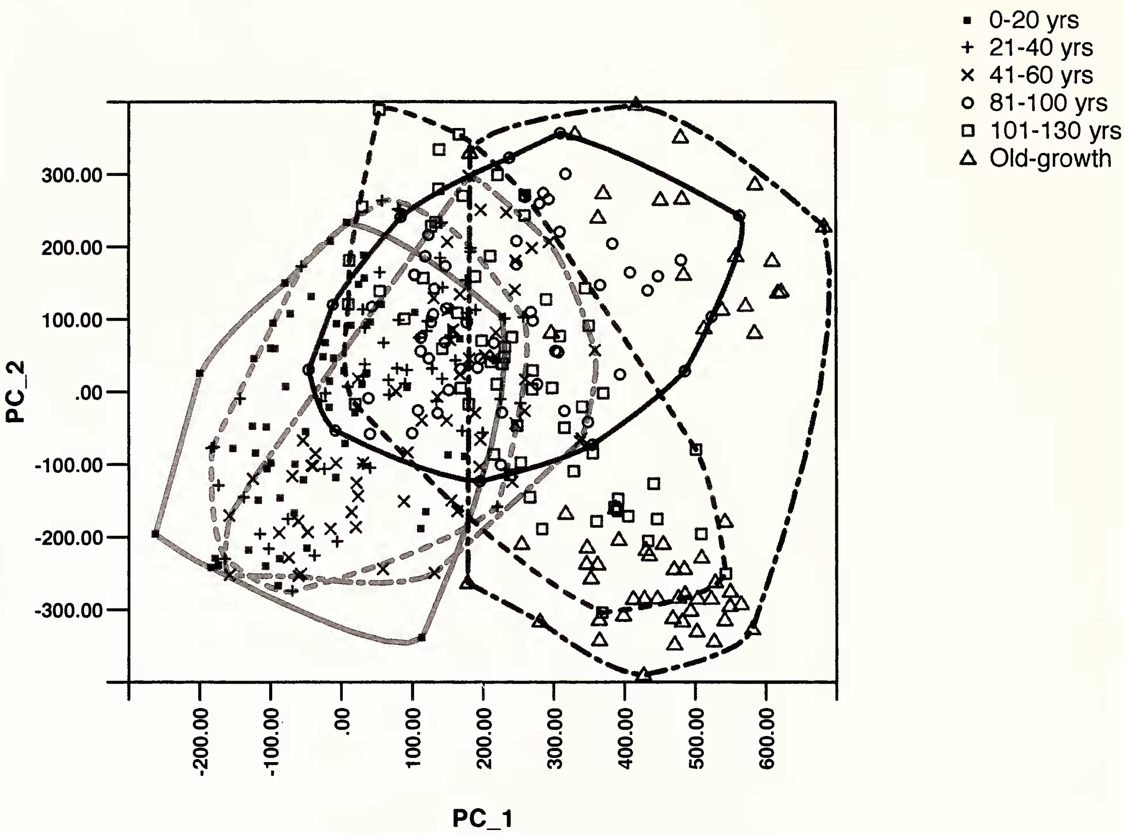

FIG. 6. Principle components for plant species across a 127-yr chronosequence of naturally regenerating *Sequoia sempervirens* stands. PC-1 explained 35.9% of variation. PC-2 explained an additional 17.4%. Convex outlines indicate post-harvest and old-growth age classes.

pletely, suggesting that reestablishment of the coast redwood understory is a lengthy process.

The ability to measure the full recovery of *S. sempervirens* stands following timber harvest was limited by the length of our chronosequence in relation to the life span of the dominant organism (>1500 yr). The study was also limited by gathering data exclusively at ground level. Considering the volume and complexity of the old-growth coast redwood canopy, the full development of a stand may require several centuries (Sillett and Baily 2003). The study of post-harvest patterns of canopy development, as well as analysis of soil organism assemblages and wildlife habitat features, could increase insight into the long-term effects of timber harvest, and

TABLE 2. NON-NATIVE PLANT SPECIES RECORDED IN SIX AGE-CLASSES IN THE CENTRAL RANGE OF THE COAST REDWOOD FOREST. The estimated date of introduction is based on the earliest specimen records for each species in northern coastal California, retrieved from the Consortium of California Herbaria (http://ucjeps.berkeley.edu/cgi-bin/get_consort).

Species	Estimated date of introduction	Oldest age-class present
Arabidopsis thaliana (L.) Heynh. (Mouse Ear Cress)	1926	41–60
Cirsium vulgare (Savi) Ten. (Common Bull Thistle)	1900	41–60
Cortaderia selloana (Schult.) Asch. & Graebn. (Pampas Grass)	1941	41–60
Hypochaeris glabra L. (Smooth Cat's Ear)	1888	41–60
Hypochaeris radicata L. (Hairy Cat's Ear)	1900	41–60
Lactuca saligna L. (Willowleaf Lettuce)	1927	0–20
Leontodon taraxacoides (Vill.) Mérat (White-Flowered Hawk Bit)	1938	21–40
Sonchus asper (L.) Hill (Spiny Sow Thistle)	1861	21–40
Stellaria media (L.) Vill. (Common Chickweed)	1876	21–40
Taraxacum officinale F. H. Wigg. (Dandelion)	1895	0–20

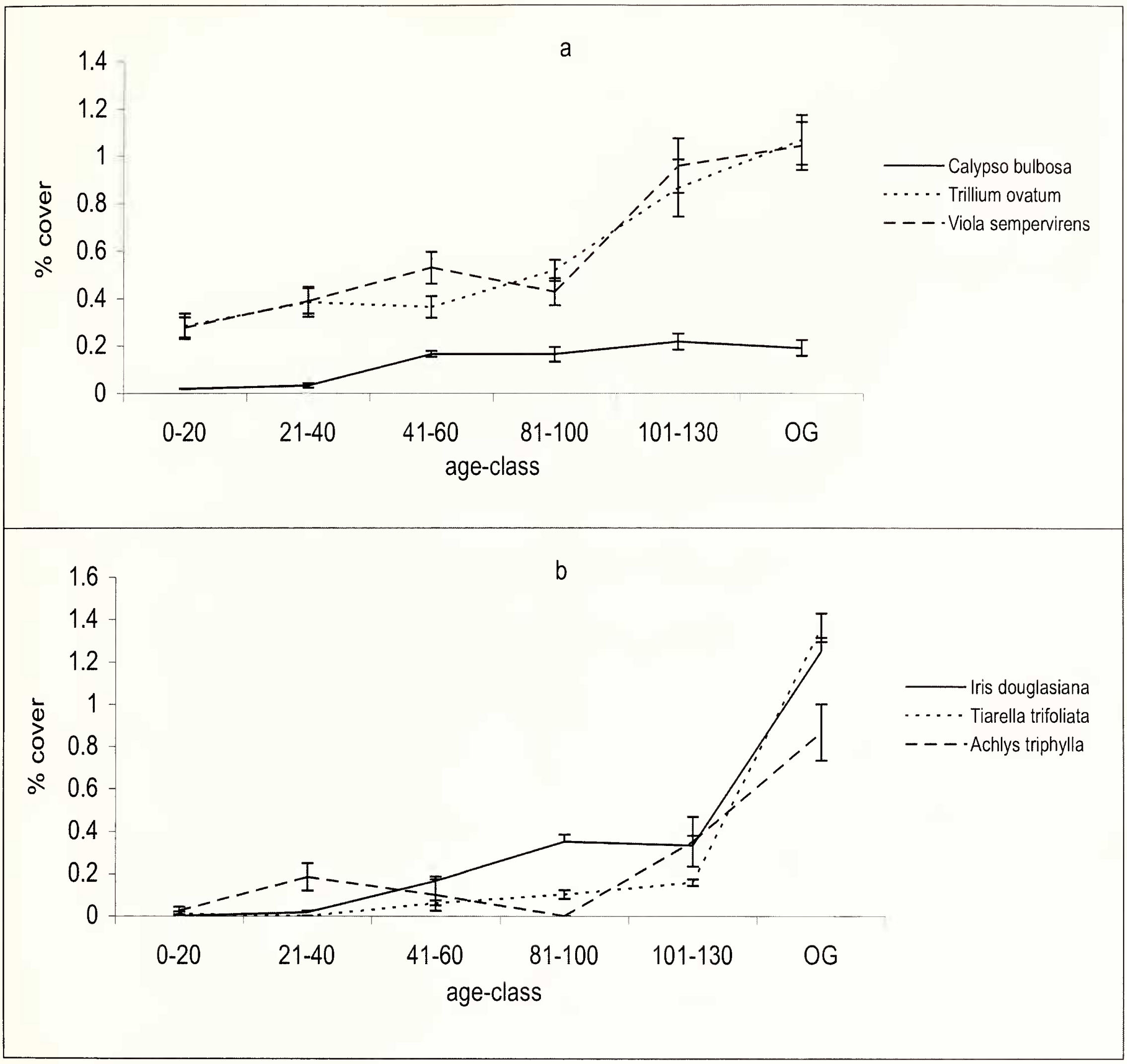

FIG. 7. Mean percent cover of coast redwood associated species on six post-harvest age-classes on a post-harvest chronosequence in the central range of the *Sequoia sempervirens* forest; error bars indicate standard error; a) represents species that reached OG equivalence, b) represents species that did not reach OG equivalence.

the regenerative potential of the entire forest community over time.

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APPENDIX 1

PLANT SPECIES RECORDED ACROSS SIX AGE-CLASSES ON A POST-HARVEST CHRONOSEQUENCE IN THE CENTRAL RANGE OF THE *SEQUOIA SEMPERVIRENS* FOREST

	Age class					
	0–20	21–40	41–60	81–100	101–130	OG
Trees (m²/plot)						
Abies grandis (Douglas ex D. Don) Lindl.	0.01	0.00	0.04	0.26	<0.01	0.02
Alnus rubra Bong.	<0.01	0.01	0.01	<0.01	0.04	0.00
Arbutus menziesii Pursh	0.11	<0.01	0.00	0.05	<0.01	0.00
Corylus cornuta var. *californica* (A. DC.) Sharp	<0.01	0.00	0.00	0.00	0.00	<0.01
Lithocarpus densiflorus (Hook. & Arn.) Rehder	0.10	0.16	0.11	0.20	0.21	<0.01
Myrica californica Cham. & Schldl.	<0.01	<0.01	<0.01	<0.01	0.00	<0.01
Pinus muricata D. Don	0.00	0.00	<0.01	0.12	<0.01	0.01
Pinus sabiniana Douglas	0.00	0.00	0.00	0.00	<0.01	0.00
Pseudotsuga menziesii (Mirb.) Franco var. *menziesii*	0.04	0.02	0.17	0.44	0.49	0.17
Salix scouleriana Hook.	<0.01	0.00	0.00	0.00	<0.01	0.00
Sequoia sempervirens (D. Don) Endl.	0.14	0.50	1.26	2.06	2.13	10.92
Taxus brevifolia Nutt.	<0.01	0.00	0.00	0.00	<0.01	0.00
Torreya californica Torr.	<0.01	<0.01	0.00	0.00	0.00	0.00
Tsuga heterophylla (Raf.) Sarg.	<0.01	<0.01	0.12	0.03	0.09	0.07
Umbellularia californica (Hook & Arn.) Nutt.	0.02	0.01	<0.01	<0.01	0.02	0.05
Shrubs (% cover/plot)						
Arctostaphylos columbiana Piper	1.08	1.30	0.00	0.00	0.00	0.00
Baccharis pilularis DC.	0.00	1.30	0.00	0.00	0.00	0.00
Berberis aquifolium Pursh	0.00	0.00	0.00	0.08	0.00	0.03

APPENDIX 1. CONTINUED.

	Age class					
	0–20	21–40	41–60	81–100	101–130	OG
Berberis nervosa Pursh	0.12	0.57	0.50	0.11	0.24	0.10
Blechnum spicant (L.) Sm.	0.00	0.15	0.10	0.43	0.10	1.18
Ceanothus thyrsiflorus Eschsch.	6.82	1.02	0.22	0.00	0.02	0.00
Euonymus occidentalis Torr.	0.00	0.00	0.00	0.00	0.00	0.09
Gaultheria shallon Pursh	0.18	0.54	0.15	2.48	1.62	7.17
Lepechinia calycina (Benth.) Epling	0.00	0.00	0.00	0.00	0.01	0.00
Lonicera hispidula Douglas	0.66	0.48	0.66	0.38	0.15	0.22
Rhododendron macrophyllum D. Don	1.24	1.24	0.38	2.46	1.78	4.28
Ribes menziesii Pursh	0.09	0.03	0.00	0.03	0.00	0.02
Rosa gymnocarpo Nutt.	0.05	0.08	0.13	0.03	0.05	0.20
Rubus leucodermis Torr. & A. Gray	0.12	0.23	0.22	0.00	0.00	0.35
Rubus parviflorus Nutt.	1.02	0.32	0.43	0.00	0.02	0.00
Rubus spectabilis Pursh	0.00	0.00	0.00	0.00	0.00	0.05
Rubus ursinus Cham. & Schldl.	0.24	0.14	1.00	0.14	0.01	0.04
Symphoricarpos albus (L.) S. F. Blake	0.00	0.00	0.01	0.00	0.02	0.00
Toxicodendron diversilobum (Torr. & A. Gray) Greene	3.21	1.04	0.80	0.47	0.58	1.53
Vaccinium ovatum Pursh	6.82	5.35	1.87	5.67	4.71	1.35
Vaccinium parvifolium Sm.	0.38	0.27	0.30	0.74	0.39	2.85
Ferns (% cover/plot)						
Adiantum aleuticum (Rupr.) C.A. Paris	0.07	0.05	0.16	0.10	0.26	0.02
Athyrium filix-femina (L.) Roth	0.00	0.05	0.16	0.10	0.26	0.02
Dryopteris arguta.(Kaulf.) Maxon	0.27	0.16	0.68	0.08	0.00	0.09
Pentagramma triangularis (Kaulf.) Yatsk., Windham & E. Wollenw.	0.58	0.18	0.10	0.02	0.02	0.02
Polypodium californicum Kaulf.	0.00	0.00	0.00	0.06	0.00	0.09
Polystichum munitum (Kaulf.) C. Presl	6.24	2.59	4.07	4.10	6.01	5.00
Pteridium aquilinum var. *pubescens* L. Underw.	0.93	1.14	0.55	1.06	0.39	1.62
Woodwardia fimbriata Sm.	0.00	0.00	0.00	0.03	0.00	3.08
Herbs (% cover/plot)						
Achlys triphylla (Sm.) DC.	0.03	0.18	0.10	0.00	0.35	0.87
Actaea rubra (Aiton) Willd.	0.02	0.01	0.09	0.02	0.15	0.11
Adenocaulon bicolor Hook.	0.05	0.00	0.08	0.08	0.07	0.80
Agoseris retrorsa (Benth.) Greene	0.01	0.05	0.00	0.00	0.00	0.00
Anaphalis margaritacea (L.) Benth. & Hook.	0.03	0.38	0.00	0.00	0.00	0.00
Anemone deltoidea Hook.	0.00	0.00	0.00	0.00	0.00	0.02
Aquilegia formosa Fisch.	0.03	0.00	0.02	0.00	0.00	0.22
Arabidopsis thaliana (L.) Heynh.	0.04	0.04	0.03	0.00	0.00	0.00
Aralia californica S. Watson	0.00	0.00	0.00	0.05	0.00	0.08
Asarum caudatum Lindl.	0.12	0.27	0.05	0.03	0.63	0.36
Calypso bulbosa (L.) Oakes	0.02	0.03	0.17	0.16	0.22	0.09
Calystegia occidentalis (A. Gray) Brummitt	0.00	0.11	0.00	0.00	0.00	0.00
Campanula prenanthoides Durand	0.17	0.07	0.18	0.01	0.02	0.11
Cardamine californica var. californica (Torr. & A. Gray) Greene	0.06	0.07	0.18	0.76	0.25	0.27
Chenopodium berlandieri Moq.	0.02	0.00	0.00	0.00	0.00	0.00
Chimaphila menziesii (D. Don) Spreng.	0.00	0.00	0.01	0.10	0.05	0.01
Chlorogalum pomeridianum (DC.) Kunth	0.01	0.00	0.07	0.00	0.00	0.00
Cirsium vulgare (Savi) Ten.	0.13	0.06	0.18	0.00	0.00	0.00
Claytonia perfoliata Willd.	0.00	0.02	0.04	0.00	0.00	0.00
Claytonia sibirica L.	0.01	0.00	0.01	0.01	0.07	0.00
Clintonia andrewsiana Torr.	0.05	0.05	0.03	0.35	0.07	0.72
Collomia heterophylla Hook.	0.00	0.01	0.00	0.00	0.00	0.00
Corallorhiza maculata Raf.	0.00	0.00	0.02	0.16	0.06	0.03
Corallorhiza striata Lindl.	0.00	0.00	0.01	0.01	0.02	0.00
Cordylanthus tenuis A. Gray spp. *tenuis*	0.01	0.00	0.00	0.00	0.00	0.00
Cortaderia selloana (Schult.) Asch. & Graebn.	0.10	0.28	0.13	0.00	0.00	0.00
Cynoglossum grande Lehm.	0.02	0.02	0.03	0.10	0.00	0.00

APPENDIX 1. CONTINUED.

	Age class					
	0–20	21–40	41–60	81–100	101–130	OG
Dicentra formosa (Haw.) Walp.	0.17	0.13	0.01	0.00	0.18	0.00
Disporum hookeri (Torr.) G. Nicholson	0.37	0.25	0.49	0.39	0.35	1.53
Epilobium angustifolium L.	0.03	0.13	0.84	0.00	0.00	0.00
Epilobium ciliatum Raf.	0.01	0.00	0.03	0.00	0.00	0.00
Equisetum arvense L.	0.04	0.00	0.02	0.03	0.07	0.05
Fragaria chiloensis (L.) Duchesne	0.05	0.00	0.03	0.00	0.00	0.00
Galium californicum Hook. & Arn.	0.03	0.07	0.00	0.00	0.00	0.22
Galium triflorum Michx.	0.36	0.23	0.61	0.41	0.23	0.72
Goodyera oblongifolia Raf.	0.00	0.00	0.00	0.20	0.00	0.02
Hemizonia corymbosa (DC.) Torr. & A. Gray	0.00	0.00	0.04	0.00	0.00	0.00
Holodiscus discolor (Pursh) Maxim.	0.03	0.00	0.00	0.00	0.00	0.00
Hypochaeris glabra L.	0.03	0.03	0.01	0.00	0.00	0.00
Hypochaeris radicata L.	0.00	0.00	0.02	0.00	0.00	0.00
Iris douglasiana Herb.	0.00	0.02	0.02	0.04	0.03	0.13
Lactuca saligna L.	0.01	0.00	0.00	0.00	0.00	0.00
Lathyrus vestitus Nutt.	0.05	0.00	0.02	0.00	0.00	0.03
Leontodon taraxacoides (Vill.) Mérat	0.01	0.03	0.00	0.00	0.00	0.00
Lithophragma glabrum Nutt.	0.00	0.00	0.00	0.00	0.00	0.00
Lotus purshianus Clem. & E.G. Clem.	0.00	0.00	0.00	0.00	0.01	0.00
Lotus stipularis (Benth.) Greene	0.32	0.14	0.22	0.04	0.03	0.04
Mimulus aurantiacus Curtis	0.12	0.00	0.00	0.00	0.00	0.00
Nemophila menziesii Hook. & Arn.	0.01	0.00	0.00	0.00	0.00	0.00
Nemophila parviflora Benth.	0.05	0.00	0.02	0.00	0.00	0.00
Oxalis oregana Nutt.	1.68	0.97	0.77	1.63	3.00	23.27
Petasites frigidus (L.) Fries	0.02	0.00	0.00	0.00	0.00	0.00
Polygala californica Nutt.	0.11	0.00	0.01	0.02	0.00	0.01
Prunella vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00
Pyrola picta Sm.	0.03	0.00	0.00	0.00	0.00	0.00
Rhamnus alnifolia L'Hér.	0.01	0.05	0.00	0.04	0.00	0.02
Rhamnus purshiana DC.	0.00	0.00	0.00	0.00	0.00	0.02
Sanicula crassicaulis DC.	0.02	0.00	0.02	0.00	0.00	0.00
Satureja douglasii (Benth.) Briq.	0.05	0.03	0.18	0.00	0.00	0.00
Scoliopus bigelovii Torr.	0.00	0.00	0.00	0.03	0.00	0.00
Scrophularia californica Cham. & Schldl.	0.02	0.20	0.00	0.00	0.00	0.00
Senecio vugares L.	0.00	0.02	0.00	0.00	0.00	0.00
Smilacina racemosa (L.) Link	0.11	0.00	0.04	0.05	0.04	0.17
Smilacina stellata (L.) Desf.	0.05	0.04	0.05	0.00	0.04	0.26
Sonchus asper (L.) Hill	0.03	0.04	0.00	0.00	0.00	0.00
Stachys bullata Benth.	0.27	0.23	0.24	0.00	0.02	0.03
Stachys ajugoides Benth.	0.00	0.00	0.00	0.08	0.00	0.58
Stellaria crispa Cham. & Schldl.	0.01	0.00	0.00	0.00	0.00	0.00
Stellaria media (L.) Vill.	0.00	0.01	0.00	0.00	0.00	0.00
Stephanomeria exigua Nutt.	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale F. H. Wigg.	0.02	0.00	0.00	0.00	0.00	0.00
Tiarella trifoliata L.	0.01	0.00	0.06	0.10	0.16	1.84
Trientalis latifolia Hook.	0.83	0.42	0.20	0.63	0.23	0.42
Trillium chloropetalum (Torr.) Howell	0.04	0.00	0.00	0.05	0.00	0.50
Trillium ovatum Pursh	0.28	0.38	0.36	0.86	0.52	1.07
Urtica dioica subsp. *holosericea* (Nutt.) Thorne	0.00	0.00	0.00	0.00	0.02	0.00
Vancouveria planipetala Calloni	0.46	0.29	0.21	0.33	0.18	0.01
Veratrum californicum Durand	0.00	0.00	0.00	0.03	0.00	0.22
Vicia americana Muhl. ex Willd.	0.01	0.00	0.00	0.00	0.00	0.00
Viola glabella Nutt.	0.00	0.00	0.00	0.02	0.08	0.93
Viola sempervirens Greene	0.28	0.40	0.53	0.96	0.44	1.03
Whipplea modesta Torr.	1.15	1.15	1.28	0.20	0.23	0.19
Yabea microcarpa (Hook. & Arn.) Koso-Pol.	0.03	0.03	0.00	0.00	0.00	0.00